APPLIED SOIL ECOLOGY 40 (2008) 370–380

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/apsoil

Cover crops and cultivation: Impacts on soil N dynamics and microbiological function in a Mediterranean vineyard agroecosystem

Kerri Steenwerth *, *K.M. Belina*

USDA/ARS, CPGRU, 1023 Wickson Hall, One Shields Avenue, CA 95616, USA

ARTICLE INFO

Article history:
Received 22 December 2007
Received in revised form
30 April 2008
Accepted 12 June 2008

Keywords:
Microbial biomass
Nitrification
Denitrification
Land use
Disturbance
Greenhouse gas
Nitrous oxide
Microbial activity
Trace gas efflux
Tillage
N mineralization
Soil organic matter

ABSTRACT

Impacts of cover crops, tillage and abiotic factors on soil nitrogen (N) dynamics, greenhouse gas emissions, and microbiological functions were investigated in a vineyard in California's Mediterranean climate. Treatments had been established in fall 2001 and were composed of two cover crops [Trios 102 (*Triticale* × *Triosecale*), ('Trios'), Merced Rye (*Secale cereale*), ('Rye')] and cultivation ('Cultivation'). Soils were sampled every 2–3 weeks from November 2005 to November 2006. Effects of season and treatment on potential nitrification and denitrification also were determined. Gravimetric water content (GWC) reflected winter and spring rainfall, and soil temperature generally did not differ among treatments. Microbial biomass N (MBN) typically was 2–3-fold greater in 'Rye' and 'Trios' than 'Cultivation' in winter and spring, but these differences among treatments disappeared in summer. Soil nitrate (NO_3^-–N) was consistently greater in cultivated soils, with little temporal change in any treatment. In contrast, soil ammonium (NH_4^+–N) in cover crop treatments was 2–3-fold greater than 'Cultivation' in winter and spring, increasing in all treatments in summer after cover crops had been mowed and 'Cultivation' had been tilled. Significant multiple linear regressions of MBN on GWC, soil temperature, NH_4^+–N and NO_3^-–N for all treatments indicated that GWC significantly explained changes in MBN. Soil temperature also was significant for 'Trios' only, but its standard coefficient value was low, indicating its lesser importance in determining MBN. Despite a significant multiple linear regression of nitrous oxide (N_2O) efflux on GWC, soil temperature, NH_4^+–N and NO_3^-–N in 'Trios' only, no single variate explained the observed variation. However, increases in N_2O were detected after both cultivation and increases in GWC from precipitation in winter, late spring, and fall. Mean daily N_2O efflux was greater in cover crops, but annual N_2O efflux was low as compared to fertilized and unfertilized annual cropping systems. Potential nitrification, N mineralization and denitrification were generally 2–4-fold greater in cover crop treatments than 'Cultivation'. Thus, cover crops enhanced the soil's capacity for supporting greater MBN, potential N mineralization, and the microbiological functions of nitrification and denitrification. Also, N dynamics appear to be more sensitive to changes in soil water content than temperature. We suggest that potential impacts of greater N_2O emissions from cover crop soils be evaluated with reference to other benefits of cover cropping, such as increased soil organic matter content, improved microbiological activity, and N availability.

Published by Elsevier B.V.

* *Corresponding author*. Tel.: +1 530 752 7535; fax: +1 530 752 0382.
E-mail addresses: ksteenwerth@ucdavis.edu, ksteenwerth@gmail.com (K. Steenwerth).
0929-1393/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.apsoil.2008.06.004

In annual agroecosystems, cover crops have been used to augment soil organic matter (SOM) content, thereby offsetting tillage-induced reductions in SOM, and increase soil nitrogen (N) retention between crop rotations (Jackson et al., 2004). Soil with greater SOM content demonstrate higher potential to immobilize and retain N (Barrett and Burke, 2000), resulting in greater potential N availability. They can support higher microbial biomass, thus serving to reduce N loss through immobilization (Jackson, 2000), but higher soil labile C has also been associated with increased capacity for denitrification (Drury et al., 1991). Loss of N can occur through tillage, which elicits short-term bursts of mineralization of organic N substrates and nitrous oxide (N_2O) efflux, potentially leading to long-term reductions in soil N content without N addition (Calderón et al., 2001; Grandy and Robertson, 2006). Cover crops are becoming increasingly popular in perennial agroecosystems like vineyards as a way to minimize erosion and increase SOM, but little is known about their potential effects on greenhouse gas emissions (i.e., N_2O) and associated N dynamics. Cover crops may be important for N retention, reducing reliance on fertilizer N additions for crop production (e.g., Jackson, 2000) and removing potential negative impacts on water quality often associated with fertilizer N use (Harrison et al., 2005). We anticipate that vineyards may have distinct soil N dynamics as compared to fertilized annual agroecosystems because cultivation occurs infrequently, and vineyard cover crops are typically unfertilized; any additions from fertilizer and irrigation are restricted to the drip zone of the grapevine after cover crops have been mowed.

The greenhouse gas N_2O is biologically produced in soils via nitrification and denitrification, two microbial processes affected by soil N availability, temperature, SOM, water content, and oxygen content (Schjønning et al., 2003; Dalal et al., 2003). It is also produced by assimilatory nitrate reduction, but this process is considered to be of minor importance. In Mediterranean climates where vineyards often exist, wet–dry cycles are common, short-term perturbations that can increase the availability of N substrates (Kieft et al., 1987; Appel, 1998), as well as elicit dynamic responses from soil microbes in terms of N mineralization, nitrification, denitrification, and N_2O efflux (Davidson, 1992; Panek et al., 2000). Certain processes may dominate in a given season, depending on prevailing conditions that influence these processes such as soil water content, substrate availability, and soil oxygen content (Dalal et al., 2003).

In order to understand how cover crops and cultivation affect soil N dynamics in a vineyard, we established our study in a Chardonnay vineyard in the Central Coast (Monterey Co., CA), a region with one of the largest contiguous stretches of vineyards in the world. The cover crop and cultivation treatments in the vineyard floor had been established 4 years previously as part of another study (Baumgartner et al., 2005). In our study, we addressed the following objective: identify effects of (1) cover crops and cultivation and (2) season (i.e., soil water content and temperature) on soil N dynamics, N availability, N_2O emissions, and microbiological function in a vineyard agroecosystem. We hypothesized that discrete management events and changes in soil water content from precipitation as well as any differences in C:N ratios of cover crop tissue would influence these soil N processes and microbiological function. Our intent was to demonstrate that cover crops improve soil N availability as compared to cultivation, a result that would be readily transferable to other perennial agroecosystems.

1. Materials and methods

1.1. Site description and experimental design

This study was conducted in a Chardonnay vineyard on Teleki 5C rootstock, planted in 1996, in the Central Coast region of California (Greenfield, Monterey County, CA). Three vineyard floor treatments in the alleys between grapevine rows had been established in late 2001 as part of another study (Baumgartner et al., 2005). These were two cover crops, Trios 102 (*Triticale* × *Triosecale*) and Merced Rye (*Secale cereale*), and a cultivated treatment. Hereafter, these will be referred to as 'Trios', 'Rye', and 'Cultivation', respectively. The experimental design was a randomized complete block, with row serving as block. Grapevine rows in this vineyard measured 506 m long, and were orientated west to east. Within each of three blocks, treatment plots each consisted of 1/6 of the row length (84.3 m), in the alleys between two rows of grapevines. There were two treatment plots of each treatment (i.e., 'Rye', 'Trios', and 'Cultivation') per block ($n = 6$ per treatment).

In the Central Coast, vineyard cover crops are typically planted in the fall at the onset of precipitation (ca. November), receive no irrigation, and grow throughout the rainy season into late spring (ca. April) while the grapevines are dormant. This study was conducted from late fall 2005 (November 2005) to late fall 2006 (November 2006), and coincided with one season of cover crop and grapevine growth. The alleys were disked prior to planting and cover crops were seed drilled into the center 1.8 m of the 2.4 m distance between grapevine rows. 'Rye' and 'Trios' were mowed in mid-April 2006 (20 April), leaving cover crop residue on the vineyard floor. 'Cultivation' was tilled approximately once every 2 months, as necessary for weed control.

Soil type was the Elder loam series (Coarse-loamy, mixed, superactive, thermic Cumulic Haploxeroll; Cook, 1978). The climate in Greenfield, CA is Mediterranean, with heavy winter rains and summer drought conditions. Average daily temperatures range from 8 °C in the winter to 19 °C in the summer; annual rainfall for the winter of 2005–2006 was 46 cm (California Irrigation Management Information System [CIMIS], url: http://www.cimis.water.ca.gov).

1.2. Vegetation and soil sampling

Vegetation and soil sampling are described in detail in Steenwerth and Belina (in press). Briefly, aboveground biomass was collected just prior to mowing and tilling in three randomly placed quadrats (0.5 m^2) per treatment replicate. Root biomass was collected from 0 to 10 cm and 10 to 20 cm (volume: 10 cm^3) (March 8, 2006), and washed to remove soil particles. Cover crop and weed roots were not separated, but roots were collected from areas with relatively fewer weeds. All plant biomass was dried at 60 °C for 48 h, and weighed. Total N of plant tissue collected just prior to mowing

was determined by combustion (Division of Agriculture and Natural Resources Analytical Laboratory DANR. University of California, Davis, url: http://www.danranlab.ucdavis.edu).

In each treatment replicate, two soil cores (0–15 cm, 500 g sample) were collected and combined every 2–3 weeks for a total of 19 sampling dates. Soil was collected between 10 a.m. and 12 p.m., placed immediately on ice, and stored within 6–8 h of collection overnight at 20 °C. All laboratory analyses were conducted within 24–48 h of sample collection. Soil temperature was taken from each plot at the time of sampling with a Li-Cor LI-6400 (Li-Cor Biosciences, Lincoln, NE, USA). To investigate seasonal changes in potential soil microbial activity, soil was collected in the same manner as biweekly samples in fall (November 30, 2005), winter (February 6, 2006), spring (May 9, 2006), and summer (August 8, 2006).

Gravimetric water content (GWC) was measured by drying a subsample at 105 °C for 24 h. Microbial biomass N (MBN) was determined by 0.5 M K_2SO_4 fumigation-extraction (Brookes et al., 1985; Vance et al., 1987). MBN was calculated according to Wu et al. (1990) and Joergensen (1996). Dissolved organic N (DON) in unfumigated MBN extracts was measured on a Shimadzu TOC-V_{CSH} unit (Shimadzu Scientific Instruments, Columbia, MD, USA. Potential net N mineralization, an assay of soil N availability, was measured by anaerobic incubation at 40 °C for 7 days (Waring and Bremner, 1964; Soon et al., 2007).

On the four seasonal sampling dates, denitrifying enzyme activity (DEA) (Tiedje, 1994), potential nitrification by slurry (Hart et al., 1994), and potential net nitrification by aerobic incubation (Robertson et al., 1999) were measured. To measure DEA, a solution of 1 mM glucose and 1 mM KNO_3 (20 mL) was added to 10 g of field moist soil in an Erlenmeyer flask (125 mL), which then was sealed with a rubber stopper with two septa and placed on an oscillating shaker (120 rpm) at 25 °C. A vacuum was applied to the flask's headspace for 1 min, followed by flushing with N_2 gas for 5 min, and repeated once. While N_2 gas was still flowing, the needle supplying N_2 gas was removed from the septum, followed by the vent needle after the flasks attained atmospheric pressure. Subsequently, 15 mL of head space gas was removed and replaced with acetylene (15 mL) to block the conversion of N_2O to N_2. Gas samples (1 mL) from the head space were collected every 15 min for a total of 60 min. An ambient air dilution method was used to store samples. Exetainer vials (6 mL) (Labco Limited, Buckinghamshire, England) were capped and pressurized by injecting two more milliliters of ambient air, followed by 1 mL of sample. This dilution method was employed to reduce the total volume of gas removed from the headspace and was accounted for in final calculations of N_2O evolution. N_2O concentrations measured on a HP 6890 gas chromatograph with an ECD detector (Agilent Technologies, Santa Clara, CA, USA) by injecting 2 mL gas using a syringe (5 mL). Standards and ambient air were placed into exetainers (6 mL) using the same dilution method described above.

Potential nitrification was described using a 24 h shaken soil-slurry method (Hart et al., 1994). Three subsamples of field moist soil (20 g) per replicate were weighed into flasks (250 mL). A solution of 1.5 mM NH_4^+ and 1 mM PO_4^{3-} (100 mL) was added to the flasks, which then were sealed with rubber stoppers with a hole (0.5 cm diameter) drilled through its center to maintain air exchange. Samples were mixed on an oscillating shaker (180 rpm) at 28 °C, and extracts from each flask were collected at 2, 4, 22, and 24 h to determine the nitrification rate. Net nitrification by aerobic incubation was measured by adjusting soil (20 g) to 40% water filled pore space. Soils were incubated at 25 °C, and soil water content was adjusted gravimetrically each week. Soil inorganic N was extracted at days 0 and 29 from three subsamples per replicate, respectively. Inorganic N from the net nitrification by aerobic incubation and the biweekly field samples was extracted with 2 M KCl. Extracts of nitrate (NO_3^-–N) and ammonium (NH_4^+–N) from biweekly soil samples, net nitrification by aerobic incubation, nitrification by slurry and potential N mineralization were measured colorimetrically (Kempers and Kok, 1989; Miranda et al., 2001) on a BioMate 3 UV-Vis spectrophotometer (Thermo Electron, Madison, WI USA). One-time measurements of percent total C and N by combustion were performed on soil collected in summer (August 30, 2006) (Division of Agriculture and Natural Resources Analytical Laboratory DANR. University of California, Davis, url: http://www.danranlab.ucdavis.edu).

1.3. *Gas sampling*

N_2O efflux was measured using a static chamber method (Folorunso and Rolston, 1984). Chambers (5.2 L) were made of polyvinyl chloride (PVC) and covered with reflective insulation to keep interior temperatures constant. PVC rings were placed into each plot at the beginning of the experiment and remained in place throughout sampling. The chambers were machine fitted for an air tight seal with the PVC rings (5 cm depth × 20 cm diameter) in the ground. The only exception to PVC ring permanency was in 'Cultivation', where rings were removed when the plots were tilled and then replaced at least 24 h prior to sampling. Beginning at approximately solar noon, gas samples (13 mL) were drawn from the sampling port every 30 min for 1 1/2 h and stored in evacuated exetainer vials (12 mL; Labco Limited, Buckinghamshire, England). Samples were analyzed for N_2O as previously described, and standards and ambient air were sampled in the same manner as the field samples prior to analysis.

1.4. *Statistical analyses*

Prior to statistical analysis, transformations were made to normalize the data as follows: GWC, soil temperature, N_2O–N efflux, potential nitrification and DEA with a square root transformation; weed biomass, NO_3^-–N, and NH_4^+–N with a $\log 10(x+1)$ transformation; cover crop biomass with a $\log 10(x)$ transformation; root biomass, root and plant percent C and N and C:N ratio, soil percent C and N and C:N ratio, and potential N mineralization were untransformed.

Using a mixed model for repeated measures analysis, effects of treatment, date and treatment-date interaction on response variables were analyzed (*proc mixed*, SAS version 8.2, SAS Institute, Cary, NC, USA). Models were blocked on row. To model variable correlation across dates, the covariance structure was either compound symmetry (used for cover crop biomass, weed biomass, GWC, soil temperature, NO_3^-–N, potential NH_4^+–N, and N_2O–N efflux) or auto regressive one (used for NH_4^+–N). Covariance structures were chosen based

on Akaike information criterion (AIC). In the cases presented where samples were collected at only one date, a general linear model was used (*proc glm*, SAS v 8.2). GLM was used for root biomass, plant percent C and N and C:N ratio, and soil percent C and N and C:N ratio. Multiple comparisons were also used to determine differences within treatments across six predetermined sampling dates. These dates were chosen based on *a priori* hypotheses that biweekly variables (e.g., MBN, inorganic N pools, potential N mineralization) would differ: (i) before and after winter rainfall (30 November 2005 vs. 13 December 2005); (ii) before and after a winter dry down event (10 January vs. 6 February); (iii) before and after mid-spring rainfall (6 February vs. 8 March); (iv) before and after mowing of cover crops or tilling the 'Cultivation' treatment (mowing: 13 April vs. 26 April; tilling: 30 May vs. 12 June); (v) before and after late spring rainfall (9 May vs. 30 May); and, (vi) before and after fall rainfall (19 September vs. 10 October). Where treatment–date interactions existed, multiple comparisons were performed to look for treatment differences within sampling dates, and the Bonferroni correction, α/n, was employed to adjust for tests of significance. Univariate statistics and multiple linear regressions of N_2O–N effluxes and MBN on GWC, soil temperature and inorganic N pools were also performed (*proc reg*, SAS v 8.2). While statistical analyses and tests of significance were performed on transformed variables in most cases (see above), all tables and graphs are presented with original data.

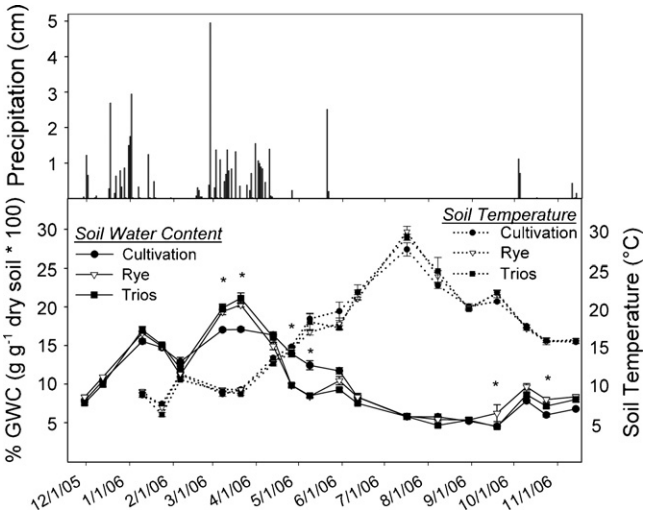

Fig. 1 – Annual precipitation and effects of cover crops and cultivation on gravimetric water content (GWC) and soil temperature. Analysis of variance (mixed model) was used to determine significance of treatments, time, and time × treatment. Asterisks (*) indicate that cover crop treatments are significantly different from 'Cultivation' on the given date.

2. Results

2.1. Soil water content and temperature

In winter (November–February), treatments had daily soil temperature that were relatively cool, ranging between 6 and 12 °C, and GWC ranged between 8 and 16% (g H_2O g^{-1} dry soil) (Fig. 1; Table 1). In spring (March–May), soil temperatures (9–19 °C) were relatively warmer and GWC ranged from 10 to 22% due to heavy rainfall over this period. In summer (June–August), daily soil temperature ranged from 20 to 30 °C and GWC was between 5 and 8%. In fall (September–November), soils were warm but cooling, with daily soil temperature ranging from 15 to 20 °C, and GWC ranged from 4 to 9%. The first rainfall occurred in early October. Typical of seasonal patterns, soil temperature increased from winter to summer and then subsequently decreased from summer to fall, but

Table 1 – Analysis of variance for effects of vineyard floor treatment and date for biweekly measurements[a]

	Effect	Treatment[b]	Date	Treatment × date
GWC[c]	F	1.2	339.24	8.11
	P	0.3895	<0.0001	<0.0001
Soil temperature	F	0.48	227.86	1.81
	P	0.6489	<0.0001	0.0221
NO_3^-–N	F	45.35	19.52	4.82
	P	0.0007	<0.0001	<0.0001
NH_4^+–N	F	41.7	21.21	2.04
	P	<0.0001	<0.0001	0.0062
MBN[c]	F	83.71	31.27	1.58
	P	<0.0001	<0.0001	0.0545
N_2O efflux	F	2.58	4.53	1.58
	P	0.1553	<0.0001	0.03
Potential N mineralization	F	139.19	6.18	1.58
	P	<0.0001	<0.0001	0.0485

[a] Analysis of variance conducted using a mixed model, $p < 0.05$.
[b] Treatments are 'Trios', 'Rye', and 'Cultivation'.
[c] Gravimetric water content (GWC), Microbial biomass nitrogen (MBN).

Table 2 – Means and standard errors of total N and C:N for roots and aboveground and biomass ($n = 6$)

	Depth (cm)	Trios	Rye
Roots			
Percent total N (g g^{-1} dry biomass)	0–10	1.60 ± 0.12	1.66 ± 0.19
	10–20	1.82 ± 0.10	1.74 ± 0.10
C:N	0–10	18.43 ± 0.63	18.88 ± 0.89
	10–20	18.38 ± 1.31	19.41 ± 1.90
Aboveground Biomass			
Percent total N (g g^{-1} dry biomass)		2.04 ± 0.10a[†]	1.63 ± 0.08b
C:N		21.27 ± 1.09a	27.206 ± 1.51b

[†] Letters indicate significant difference according to ANOVA and Tukey's test for mean separation, $p < 0.05$.

did not differ among treatments. GWC reflected precipitation events but did not differ by treatment except in spring (March), when precipitation frequency was high, and soil water content was greater in the cover crops than 'Cultivation'.

2.2. Vegetation and soil characteristics

No difference in total N and C:N ratio existed between roots of Trios and Rye at either depth (Table 2). Total N of aboveground biomass was 1.3-fold greater in Trios than Rye, but the aboveground C:N ratio of Rye was 1.3-fold greater than Trios. Total soil N in 'Trios' was 1.2-fold greater than in 'Rye', and 1.4-fold greater than in 'Cultivation', but did not differ between 'Cultivation' and 'Rye' (percent N, mean ± S.E.: 'Trios' 0.120 ± 0.004, 'Rye' 0.098 ± 0.005, 'Cultivation' 0.088 ± 0.003 g N g^{-1} dry soil, $n = 6$, $p < 0.05$). Soil C:N ratios did not differ between 'Rye' and 'Trios', but cover crop treatments were greater than 'Cultivation' (C:N, mean ± S.E.: 'Trios' 9.20 ± 0.28, 'Rye' 9.67 ± 0.68, 'Cultivation' 8.16 ± 0.24, $n = 6$, $p < 0.05$). In summary, (1) differences in biomass and C:N ratios between Trios and Rye plants existed in the above ground portion; and (2) a slight but significantly higher soil N content was observed in 'Trios' as compared to 'Rye'.

2.3. Soil inorganic N pools

Soil inorganic N pools reflected sampling date, cover crop growth, and management practices, and these pools tended to be relatively low in all treatments (Fig. 2a; Table 1). Except in early winter, when soil NO_3^-–N was greatest approximately 1 month after cover crop and weed incorporation, 'Rye' and 'Trios' consistently had 2–3 times less NO_3^-–N than 'Cultivation'. After rainfall in early winter and when plant growth was minimal, NO_3^-–N decreased 12–15-fold in all treatments. Pools remained at this level in both cover crop treatments until 1–2 weeks after mowing, when soil NO_3^-–N approximately doubled in 'Rye' and 'Trios' ($p < 0.05$). In 'Cultivation', NO_3^-–N increased 2-fold 3 weeks after tilling, but decreased by the subsequent sampling date ($p < 0.05$). Nitrate pools exhibited little change over summer, although 'Cultivation', which experienced one tillage pass during this period, had slightly higher concentrations than 'Rye' and 'Trios'; this difference disappeared after fall precipitation.

Although values tended to be low, NH_4^+–N pools in cover crop treatments were 2–3 times greater than 'Cultivation' in winter and spring (Fig. 2b; Table 1). Ammonium pools increased from early winter to mid-spring in the cover crops but not in 'Cultivation' ($p < 0.05$). As cover crops approached peak growth in late spring, NH_4^+–N pools fell in the cover crop treatments ($p < 0.05$). In summer, after cover crops were mowed and 'Cultivation' was tilled, soil NH_4^+–N increased in all treatments ($p < 0.05$), and no difference was observed among treatments. With the influx of fall rains (October), soil NH_4^+–N decreased in all treatments ($p < 0.05$), and, again, no difference was detected among treatments. Thus, soil inorganic N pools differed by cover crop and 'Cultivation' treatments and sampling date.

2.4. Soil microbial biomass N

In general, microbial biomass N was greater in 'Trios' and 'Rye' than 'Cultivation' and reflected trends in soil water content (Fig. 2c; Table 1). In spring, MBN typically was 2–3-fold greater in 'Rye' and 'Trios' than 'Cultivation'. Differences in MBN between the respective cover crops were also observed in spring. MBN was 1.6–2-fold greater in 'Trios' than 'Rye' and 'Cultivation' on two sampling dates in late winter (late January–February). In early spring (March), 'Rye' exceeded 'Trios' and 'Cultivation' by 1.4- and 2.7-fold, respectively. After cover crops had been mowed and as soil water content decreased from winter to summer, MBN in 'Rye' and 'Trios' decreased to similar levels as 'Cultivation' ($p < 0.05$). With the increase in soil water content due to fall rain, MBN doubled in 'Rye' and 'Trios' but no response occurred in 'Cultivation'. No significant response of MBN to cultivation was observed. When comparing MBN before and after mowing, a decrease occurred, but a similar decrease was observed on these same dates in 'Cultivation' ($p < 0.05$).

Significant linear multiple regressions occurred in all treatments when MBN was regressed onto GWC, soil temperature, soil NO_3^-–N and NH_4^+–N ('Rye' adj. $r^2 = 0.713$, $p < 0.0001$; 'Trios' adj. $r^2 = 0.559$, $p < 0.0001$; 'Cultivation' adj. $r^2 = 0.526$, $p < 0.0001$; data not shown). In 'Cultivation' and 'Rye', only GWC was significant in explaining the variation in MBN ($p < 0.0001$). In 'Trios', both soil temperature ($p = 0.02$) and GWC ($p < 0.0001$) were significant in explaining variation in MBN, but GWC had the highest contribution to explaining the variation in MBN (standardized estimates: GWC, 0.729; soil temperature, −0.085). In all treatments, a positive relationship existed between MBN and GWC ($p < 0.0001$; Pearson's correlation coefficient: 'Rye' $r = 0.824$, 'Trios' $r = 0.734$, 'Cultivation'

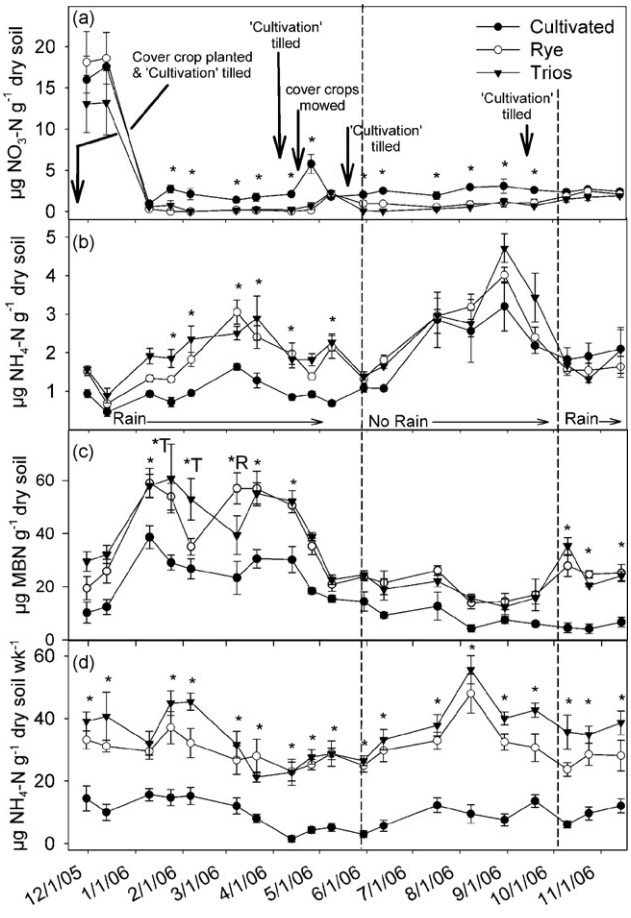

Fig. 2 – Biweekly measures of soil nitrate (NO_3^-–N) (a), ammonium (NH_4^+–N) (b), microbial biomass nitrogen (MBN) (c), and potential net mineralization (i.e., nitrogen (N) availability) (d). Analysis of variance (mixed model) was used to determine significance of treatment, time, and time × treatment. Asterisks (*) indicate that cover crop treatments are significantly different from 'Cultivation' on the given date. The symbol "*R" indicates that 'Rye' was greater than 'Cultivation' and 'Trios' on that given date, and "*T" indicates that 'Trios' was greater than 'Cultivation' and 'Rye' on that respective date. Arrows indicate time of management event. Dashed vertical lines demarcate periods of rainfall.

$r = 0.697$). In 'Trios', soil temperature was negatively associated with MBN ($p < 0.0001$; Pearson's correlation coefficient: 'Trios' $r = -0.716$).

2.5. *Soil N availability and potential microbial activity*

The greater potential N mineralization rates in the cover crop treatments demonstrated that these soils had greater potential N availability (Fig. 2d; Table 1). Despite differences in C:N ratios in aboveground plant tissue, potential N mineralization did not differ between cover crops. Potential N mineralization, an indicator of potential soil N availability, was 3–4-fold greater in the cover crops than 'Cultivation', with little difference between 'Rye' and 'Trios' regardless of sampling date. No effect after mowing or tilling on potential N mineralization was observed.

Potential N mineralization did not change in any treatment before and after increases in soil moisture from winter rainfall. In spring, potential N mineralization was highest in 'Trios', decreasing by half after spring rainfall ($p < 0.05$). No change in potential N mineralization was observed over this same period in 'Rye' and 'Cultivation'. In summer, potential N mineralization also increased only in 'Rye' and 'Trios, peaking in August ($p < 0.05$). No change in potential N mineralization was observed before and after changes in soil water content from initial fall rains ($p < 0.05$).

Patterns in seasonal measures of potential microbial activity showed that both date and treatment had significant effects (Table 3; Fig. 3a–c). Potential nitrification by soil slurry, a measure of potential enzymatic activity, was 2-fold greater in 'Rye' and 'Trios' than 'Cultivation' (mean ± S.E.: 'Rye', 8.45 ± 1.04; 'Trios', 9.09 ± 1.03; 'Cultivation', 4.08 ± 0.66 μg NO_3^-–N g^{-1} d^{-1}, $n = 24$). Potential nitrification rates were greatest in summer when MBN was lowest, followed immediately by winter and fall when soils had greater soil water content (mean ± S.E.: summer, 11.73 ± 0.98; winter, 9.26 ± 0.82; fall, 6.53 ± 0.77; spring, 1.31 ± 0.22 μg NO_3^-–N g^{-1} d^{-1}, $n = 18$, $p < 0.05$). They were lowest in spring, after cover crops had been mowed and weeds had been tilled in 'Cultivation'. Unlike potential nitrification assays, net nitrification rates by aerobic incubation did not respond consistently among date and treatment. 'Trios' was 2-fold greater than 'Cultivation' in winter and 2-fold greater than both 'Rye' and 'Cultivation' in fall ($p < 0.05$); in spring and summer, no difference was observed among treatments. Similar to

Table 3 – Analysis of variance for effects of vineyard floor treatment and season for seasonal measurements[a]

	Effect	Treatment[b]	Season[b]	Treatment × season
Potential nitrification[c]	F	65.81	116.00	1.94
	P	<0.0001	<0.0001	0.099
Net nitrification[c]	F	9.9	7.01	4.29
	P	0.0005	0.0008	0.002
DEA[c]	F	40.62	17.88	3.03
	P	<0.0001	<0.0001	0.0158

[a] Analysis of variance conducted using a mixed model, $p < 0.05$.
[b] Treatments are 'Trios', 'Rye', and 'Cultivation'. Season includes 'Fall', 'Winter', 'Spring' and 'Summer'.
[c] Denitrifying enzyme potential (DEA), 'Potential nitrification' conducted by slurry method, 'Net nitrification' conducted by aerobic incubation.

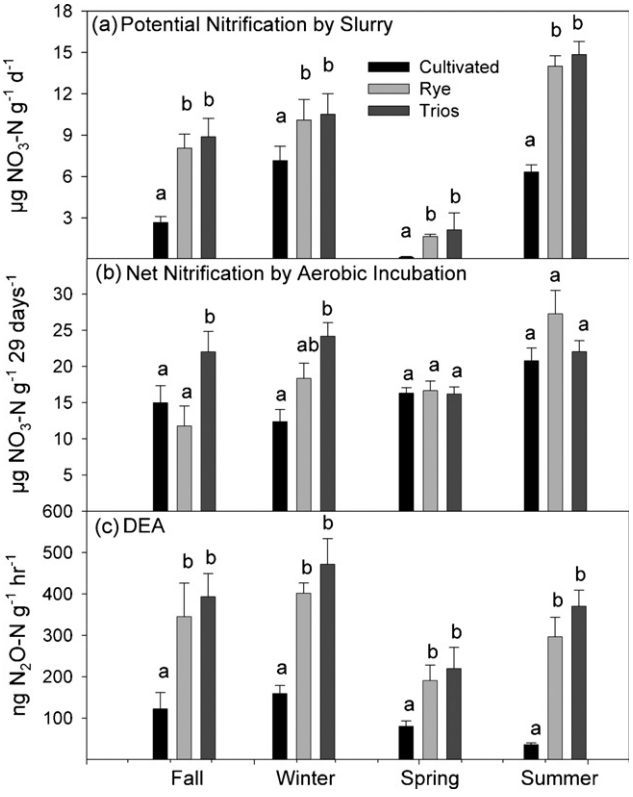

Fig. 3 – Effects of cover crops and cultivation on nitrification potential by slurry (a), net nitrification by aerobic incubation (b) and denitrifying enzyme potential (DEA) (c) in four seasons. Analysis of variance (mixed model) was used to determine significance of treatments, time, and time × treatment. Letters indicate significant differences among treatments within the respective season.

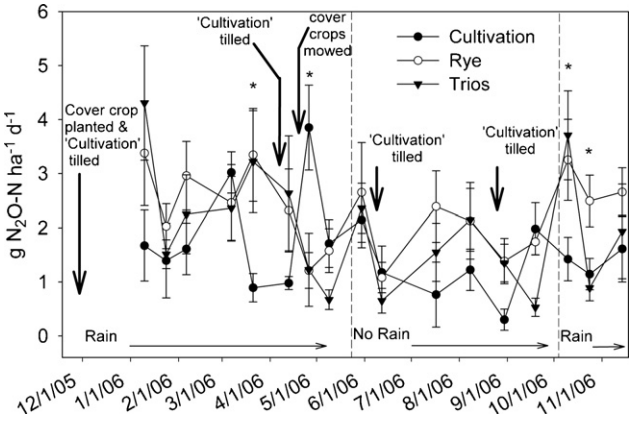

Fig. 4 – Effects of cover crops and cultivation on nitrous oxide (N_2O–N) efflux. Analysis of variance (mixed model) was used to determine significance of treatments, time, and time × treatment. Asterisks (*) indicate that cover crop treatments are significantly different from 'Cultivation' on the given date. Arrows indicate time of management event. Dashed vertical lines demarcate periods of rainfall.

potential nitrification by slurry, DEA was 2–8-fold greater in both cover crops than 'Cultivation' within each date ($p < 0.05$). Denitrifying enzyme potential was greater in winter than spring in 'Rye', greater in winter and summer than spring in 'Trios', and greater in winter than summer in 'Cultivation' ($p < 0.05$). Thus, in each treatment, DEA typically was greater in seasons that had higher soil water content.

2.6. *Soil N_2O efflux*

Soil N_2O efflux was sensitive to treatment and sampling date (Fig. 4; Table 1). Daily mean N_2O–N efflux was greater in 'Rye' and 'Trios' than 'Cultivation' (mean ± S.E.: 'Rye' 2.31 ± 0.15; 'Trios' 1.94 ± 0.17; 'Cultivation' 1.59 ± 0.13 g N_2O–N ha^{-1} d^{-1}, $n = 102$, $p < 0.05$). In early winter, N_2O–N efflux was high in all treatments, corresponding to the high NO_3^-–N pools and soil water content in all treatments, but this flux decreased by the subsequent sampling date ($p < 0.05$). In spring (April 13), approximately 2 weeks after the highest observed soil water content, N_2O–N efflux was approximately 3-fold greater from 'Rye' and 'Trios' than 'Cultivation' ($p < 0.05$). After mowing, N_2O–N efflux decreased 3-fold in 'Rye' and 'Trios'. After 'Cultivation' was tilled, N_2O–N efflux from 'Cultivation' increased 4-fold from the previous sampling date, and was also 4-fold greater than the efflux rates observed in the cover crops ($p < 0.05$). Despite the low soil water contents in summer, N_2O–N efflux rates (1–2 N_2O–N ha^{-1} d^{-1}) were detected, which corresponded to increases in DON (data not shown), potential N mineralization, and NH_4^+–N pools (Fig. 2b and d). After the initial fall rains, N_2O–N efflux increased approximately 2–4-fold in 'Rye' and 'Trios', decreasing by the subsequent sampling date ($p < 0.05$). No temporal change was observed in 'Cultivation' in response to fall rain.

Surprisingly, relationships among GWC, soil temperature, NO_3^-–N and NH_4^+–N pools, and potential N mineralization with N_2O–N efflux were not evident by multiple linear regression. Regression analysis was significant only for 'Trios', although no single variate was significant in explaining the variation in N_2O–N efflux ('Rye' adj. $r^2 = 0.103$, $p = 0.074$; 'Trios' adj. $r^2 = 0.232$, $p < 0.0001$; 'Cultivation' adj. $r^2 = 0.070$, $p = 0.270$; data not shown). GWC had the highest contribution to explaining the variation in N_2O–N efflux in 'Trios', followed by soil temperature (standard estimate: GWC, 0.293; soil temperature, −0.126).

3. Discussion

3.1. *Relationships between inorganic N pools, MBN and N availability*

We attribute temporal dynamics to abiotic factors, decomposition, and/or microbial N immobilization. Incorporation and subsequent decomposition of cover crop and weed biomass during fall disking contributed to the higher concentration of NO_3^-–N in early winter (Lundquist et al., 1999; Rochette et al., 2004). In early winter, the strong decrease in NO_3^-–N in the absence of substantial cover crop and weed growth can be attributed to leaching or trace gas efflux in response to precipitation (Davidson, 1992), a supposition

further supported by the high N_2O efflux observed at that same sampling date. Subsequently, little temporal change in NO_3^-–N was observed among treatments. In winter and spring, N immobilization facilitated low inorganic N concentrations, as indicated by greater MBN in all treatments during those seasons. In summer, increases in NH_4^+–N corresponded to decreases in MBN and increasing dissolved organic N and C (Steenwerth and Belina, in press), suggesting that MBN turnover and cover crop-derived organic matter contributed to these pools. Although plant N uptake was not directly measured, the similarity in cover crop N dynamics despite differences in phenology of aboveground plant growth suggests that N dynamics (including MBN) partly were influenced by cover crops sown in the previous four years (Steenwerth and Belina, in press). This concept is also supported by the increase in MBN in the cover crop treatments that occurred after the increase in soil water content in fall as compared to the absence of a response in 'Cultivation'.

Wet–dry cycles common in Mediterranean climates can elicit strong ephemeral increases in inorganic N pools (Appel, 1998). Under mild soil rewetting conditions in agricultural and grassland soils from this same geographical region, increases in inorganic N were not previously observed (Steenwerth et al., 2005). Pulleman and Tietama (1999) also did not observe increases in net nitrification from forest litter that had been dried and then rewet. The lack of strong temporal change in NO_3^-–N and the mild increase in NH_4^+–N when soil water content increased (i.e., in spring) may partly be attributed to its potential rapid consumption by microbial immobilization (Jackson et al., 1989; Burger and Jackson, 2003). Corresponding fluctuations in MBN, N_2O–N efflux, and NH_4^+–N pools in winter and spring in cover crop soils (see Fig. 2) also suggest that mineralized N may have been immobilized by MBN and/or nitrified in response to increases in soil water content from precipitation. In some cases, soil microorganisms can preferentially immobilize NO_3^-–N, especially when soil NH_4^+–N concentrations are low, which may explain why few increases in soil NO_3^-–N were observed (Burger and Jackson, 2003). In support of this idea, microbial biomass N in the cover crop soils was consistently greater during winter and spring. MBN also responded more dynamically to changes in soil water content from precipitation in 'Cultivation', as demonstrated by the increase in MBN only in cover crop soils after fall precipitation. The sensitivity of MBN to changes in soil moisture is further bolstered by the positive and significant association between MBN and GWC in all treatments. Although soil temperature was significant in explaining variation in MBN in 'Trios', its standard estimate indicates that it was much less important than GWC in doing so.

In comparison to other agroecosystems in the same geographical region, concentrations of MBN in the vineyard cover crop and cultivated soils were 3–4-fold and 1.5-fold greater, respectively, than an annual cole crop system employing minimum tillage, cover crops and annual organic matter applications (Jackson et al., 2004). The vineyard cover crop and cultivated soil also had 5–6-fold and 1–2-fold greater potential N mineralization, or potential N availability, respectively, than the same annual cropping system. This, and the fact that the cover crop soils supported greater MBN as compared to the cultivated soil, indicates that the less intensive vineyard floor management practices enhanced soil N availability. Also, the consistently greater pool of NO_3^-–N and lower MBC in the cultivated soil as compared to the cover crop soils suggests that soil microorganisms were C-limited in 'Cultivation' (Steenwerth and Belina, in press). In conjunction with the higher MBN in cover crop soils, this highlights the strong effect of cover crop-derived C inputs on soil N immobilization.

3.2. *Impacts of management and season on N_2O efflux*

Discrete management practices influenced N_2O efflux. For example, after spring tillage in 'Cultivation', increases in N_2O efflux, NH_4^+–N and NO_3^-–N and a decrease in MBC occurred in concert, as compared to undisturbed cover crop soils (Steenwerth and Belina, in press). This suggests that tillage enhanced N_2O efflux through microbial turnover and decomposition of weed biomass (Calderón et al., 2001; Jackson, 2000). Although N mineralization of plant biomass can occur within the first week of cover crop mowing and incorporation (Wyland et al., 1996; Dahlin et al., 2005), substantial mineralization of plant N was likely delayed until fall disking, as suggested by the high NO_3^-–N concentrations observed shortly after cover crop incorporation (see Fig. 2a, December). In the absence of significant plant growth, the high NO_3^-–N pools and associated N_2O efflux in early winter in all treatments suggests that timing of plant residue incorporation is crucial to both minimize loss via N_2O efflux or leaching (Dahlin et al., 2005) and provide inorganic N to grapevines through decomposition, especially as it has been demonstrated that grapevines can access soil inorganic N in the alleys (King and Berry, 2005).

Nitrous oxide emissions from nitrification and denitrification can have high temporal and spatial heterogeneity, which may contribute to the high variability and absence of correlation between measured parameters and N_2O efflux (Christensen et al., 1990; Davidson, 1992; Mummey et al., 1997). The lack of relationship between inorganic N pools and N_2O efflux is consistent with Rochette et al. (2004), who suggested that the inorganic N pool can be a poor indicator of N_2O production, as observed in their study that documented relationships between inorganic N pools, abiotic factors, and N_2O efflux after incorporation of various unfertilized crops. Non-linear multiple regressions of N_2O–N on just GWC and soil temperature by treatment using a parabolic model (data not shown) showed no significant relationship. However, N_2O efflux was sensitive to precipitation, as exhibited by the strong increase in N_2O efflux in fall and late spring just after increases in soil water content from rainfall.

By integrating the area under the N_2O–N efflux curve, total annual N_2O–N efflux can be estimated. Efflux tended to be greater in the cover crop treatments than 'Cultivation' (mean ± S.E.: 'Rye' 693.9 ± 73.81; 'Trios' 565.3 ± 35.8; 'Cultivation' 466.7 ± 39.7 g N_2O–N ha^{-1}, $n = 6$). Nitrous oxide efflux from the cover crops was relatively low in comparison to other cropping systems, even those without fertilizer additions. For example, N_2O emission rates from unfertilized crops (e.g., timothy, alfalfa, and soybean) grown in eastern Canada ranged between 0.75- and 3-fold of the N_2O efflux observed from the vineyard cover crops, but their estimates were made

over just 7 months (Rochette et al., 2004). Estimates of total N_2O efflux from the vineyard also fall within the low range of emission rates observed in ley cropping systems using ryegrass (*Lolium perenne*) and subterranean clover (*Trifolium subterraneum*) in Australia (Dalal et al., 2003). In comparison to annual cropping systems of corn–soybean–wheat, N_2O efflux rates from tilled and untilled soils in the Midwest (USA) measured over a 12 year period were 1.6–3-fold greater than those observed in this vineyard system (Grandy et al., 2006). It must be recognized that these estimates from the vineyard cover crops were collected over one year and interannual variation is expected depending on cover crop growth as well as abiotic factors like soil water content and temperature.

3.3. *How did treatments affect the capacity for N mineralization, nitrification, and denitrification?*

Cover crop soils supported greater potential denitrification, nitrification and mineralization than cultivated soils, indicating that cover crop soils have a higher enzymatic capacity for these processes than cultivated soil. The increased potential denitrification rates in the cover crop treatments correspond to increases in labile C, consistent with other studies (Steenwerth and Belina, in press; Dalal et al., 2003). Temporal shifts in potential N mineralization paralleled changes in dissolved organic C in all treatments, suggesting its close link to this pool (Steenwerth and Belina, in press). Following suit, the capacity for nitrification was greater in cover crop soils than 'Cultivation'. Lower aboveground biomass C:N ratio in 'Trios' may have contributed to the greater nitrification rates in 'Trios' in fall and spring, emphasizing either the importance of plant tissue composition on N availability or vice versa, the effect of soil N availability on plant tissue. For comparison, nitrification potential values from these vineyard cover crop soils are similar to an annual agricultural rotation utilizing cover crops (Fortuna et al., 2003).

We hypothesized that the relative dominance of potential denitrification or potential nitrification in a given season would suggest which process likely contributed to N_2O efflux in a given season, but our findings do not firmly support this. For instance, seasonal conditions of greater soil water content in winter appeared to confer higher denitrifying potential to all soils, regardless of treatment. On the other hand, in all treatments in spring, neither DEA nor nitrification potentials were as high as in the other seasons, a trend which does not lend support to our hypothesis. Substrate limitation due to N immobilization and plant N uptake may have contributed to this outcome, but similar net nitrification rates by aerobic incubation and the decrease in MBN among all treatments suggests that soil water content, and not substrate, was limiting; soil water content decreased severely in late spring, at the time of the seasonal sampling.

In summer, the greater value of potential nitrification for all treatments as compared to the intermediate DEA rates suggests that conditions such as low soil water content may have favored the enzymatic potential for nitrification over denitrification. This suggests that increases in field-based N_2O efflux in cover crop treatments over summer and the corresponding increases in soil NH_4^+–N likely were linked to nitrification. Soil water content reached the lowest levels in summer, and decreases in soil respiration as well as microbial biomass C and N also suggest that soil water content was limiting (Steenwerth and Belina, in press). Lack of increase in NO_3^-–N pools and limiting soil water content suggest that abiotic N_2O efflux may have occurred, although it is unclear whether conditions were satisfied for this process to occur (e.g., relatively low pH) (Venterea and Rolston, 2000).

4. Conclusion

This study represents a first step in documenting differences in soil N dynamics and nitrous oxide efflux in vineyards, a perennial agroecosystem widely established in California and other regions of the world. Clearly, in this vineyard, cover crops enhanced soil N dynamics and microbiological functions of N mineralization, nitrification and denitrification, as measured by assays of potential microbial activity. The similarity in N dynamics between the cover crops indicated that both species have similar potentials for enhancing N dynamics and soil N availability, and microbial functions of N mineralization, nitrification, and denitrification. In contrast, using cultivation for weed control diminished the soil's capacity for these processes, as well as total soil N content, and should be minimized in vineyard floor management and in other perennial agroecosystems. We also demonstrated that soil N dynamics appear to be more sensitive to changes in soil water content than temperature.

In comparison to N fertilized and some unfertilized agroecosystems, total N_2O efflux from cover crops and tilled soils was relatively low. With the increasing need to create inventories of greenhouse gas emissions from perennial cropping systems, we caution that while the cover crops tended to have greater N_2O efflux as compared to the cultivated soil, plant N uptake and leaching must be included to complete the system's N budget prior to determining which management practice retains or loses greater soil N. Increased N_2O efflux must also be evaluated relative to potential decreases in fossil fuel use from modified vineyard floor management practices as well as associated increases in soil organic matter content. For instance, in this vineyard, total soil carbon content was 40–50% greater in soils supporting five consecutive years of annual cover crops than in soils that had been continuously cultivated (Steenwerth and Belina, in press). Nonetheless, greater MBN in cover crop soils suggests that soil microbial biomass provided a larger sink for soil N than existed in cultivated soils, which could be important for both long-term retention of soil N and grapevine health, especially given that grapevines can access soil N in the alleys where cover crops are grown. Furthermore, the high cost of fossil fuels used in the production of N fertilizer could limit its current use to precisely control N delivery to cash crops, emphasizing that utilizing cover crops to enhance soil N availability and the capacity of microbiological functions must be considered for vineyards and other perennial and annual agroecosystems.

Acknowledgements

We thank Joshua Hunt, Novella Nelson, and Eli Carlisle for field and laboratory assistance; Daryl Salm and Valley Farm Management for maintaining field treatments and providing use of farm equipment; Paraiso Winery for providing the field site; Dr. Bruce Mackey of the USDA/ARS for guidance in statistical analysis; and Richard Smith and Larry Bettiga of University of California Cooperative Extension, who established the original field trial.

REFERENCES

Appel, T., 1998. Non-biomass soil organic N—the substrate for N mineralization flushes following soil drying-rewetting and for organic N rendered $CaCl_2$-extractable upon soil drying. Soil Biol. Biochem. 30, 1445–1456.

Barrett, J.E., Burke, I.C., 2000. Potential nitrogen immobilization in grassland soils across a soil organic matter gradient. Soil Biol. Biochem. 32, 1707–1716.

Baumgartner, K., Smith, R.F., Bettiga, L., 2005. Weed control and cover crop management affect mycorrhizal colonization of grapevine roots and arbuscular mycorrhizal fungal spore populations in a California vineyard. Mycorrhiza 15, 111–119.

Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil-nitrogen—a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biol. Biochem. 17, 837–842.

Burger, M., Jackson, L.E., 2003. Microbial immobilization and nitrate in relation to ammonification and nitrification rates in organic and conventional cropping systems. Soil Biol. Biochem. 35, 29–36.

Calderón, F.J., Jackson, L.E., Scow, K.M., Rolston, D.E., 2001. Short-term dynamics of nitrogen, microbial activity, and phospholipid fatty acids after tillage. Soil Sci. Soc. Am. J. 65, 118–126.

Christensen, S., Simkins, S., Tiedje, J.M., 1990. Temporal patterns of soil denitrification; their stability and causes. Soil Sci. Soc. Am. J. 54, 1614–1618.

Cook, T.D., 1978. Soil Survey of Monterey County, California. United States Department of Agriculture, Soil Conservation Service, U.S. Forest Service and University of California Agricultural Experiment Station, Washington, D.C., pp. 15–16, 34, 224–225.

Dahlin, S., Kirchmann, H., Katterer, T., Gunnarsson, S., Bergström, L., 2005. Possibilities for improving nitrogen use from organic materials in agricultural cropping systems. Ambio 34, 288–295.

Dalal, R.C., Want, W., Robertson, G.P., Parton, W.J., 2003. Nitrous oxide emission from Australian agricultural lands and mitigation options: a review. Aust. J. Soil Res. 41, 165–195.

Davidson, E.A., 1992. Sources of nitric oxide and nitrous oxide following wetting of dry soil. Soil Sci. Soc. Am. J. 56, 95–102.

Drury, C.F., McKeeney, D.J., Findlay, W.I., 1991. Relationships between denitrification, microbial biomass and indigenous soil properties. Soil Biol. Biochem. 23, 751–755.

Folorunso, O.A., Rolston, D.E., 1984. Spatial variability of field-measured denitrification gas fluxes. Soil Sci. Soc. Am. J. 48, 1214–1219.

Fortuna, A., Harwood, R.R., Robertson, G.P., Fisk, J.W., Paul, E.A., 2003. Seasonal changes in nitrification potential associated with application of N fertilizer and compost in maize systems of southwest Michigan. Agric. Ecosyst. Environ. 97, 285–293.

Grandy, A.S., Robertson, G.P., 2006. Initial cultivation of a temperate-region soil immediately accelerates aggregate turnover and CO_2 and N_2O fluxes. Glob. Change Biol. 12, 1507–1520.

Grandy, A.S., Loecke, T.D., Parr, S., Robertson, G.P., 2006. Long-term trends in nitrous oxide emissions, soil nitrogen, and crop yields of till and no-till cropping systems. J. Environ. Qual. 35, 1487–1495.

Harrison, J.A., Matson, P.A., Fendorf, S.E., 2005. Effects of diel oxygen cycle on nitrogen transformations and greenhouse gas emissions in a eutrophied subtropical stream. Aquatic Sci. 67, 308–315.

Hart, S.C., Stark, J.M., Davidson, E.A., Firestone, M.K., 1994. Nitrogen mineralization, immobilization, and nitrification. In: Bigham, J.M., Mickelson, S.H. (Eds.), Methods of Soil Analysis. Part 2. Microbiological and Biochemical Properties. Soil Science Society of America, Madison, WI, USA, pp. 1006–1014.

Jackson, L.E., 2000. Fates and losses of nitrogen from a nitrogen-15-labeled cover crop in an intensively managed vegetable system. Soil Sci. Soc. Am. J. 64, 1404–1412.

Jackson, L.E., Schimel, J.P., Firestone, M.K., 1989. Short-term partitioning of ammonium and nitrate between plants and microbes in an annual grassland. Soil Biol. Biochem. 21, 409–415.

Jackson, L.E., Ramirez, I., Yokota, R., Fennimore, S.A., Koike, S.T., Henderson, D.M., Chaney, W.E., Calderón, F.J., Klonsky, K., 2004. On-farm assessment of organic matter and tillage management on vegetable yield, soil, weeds, pests, and economics in California. Agric. Ecosyst. Environ. 103, 443–463.

Joergensen, R.G., 1996. The fumigation-extraction method to estimate soil microbial biomass: calibration of the k(EC) value. Soil Biol. Biochem. 28, 25–31.

Lundquist, E.J., Jackson, L.E., Scow, K.M., Hsu, C., 1999. Changes in microbial biomass and community composition, and soil carbon and nitrogen pools after incorporation of rye into three California agricultural soils. Soil Biol. Biochem. 31, 221–236.

Kempers, A.J., Kok, C.J., 1989. Re-examination of the determination of ammonium as the indophenol blue complex using salicylate. Anal. Chim. Acta 221, 147–155.

Kieft, T., Soroker, E., Firestone, M.K., 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biol. Biochem. 19, 119–126.

King, A.P., Berry, A.M., 2005. Vineyard $\delta^{15}N$, nitrogen and water status in perennial clover and bunch grass cover crop systems of California's central valley. Agric. Ecosyst. Environ. 109, 262–272.

Miranda, K.M., Espey, M.G., Wink, D.A., 2001. A rapid, simple spectrophotometric method for simultaneous detection of nitrate and nitrite. Nitric Oxide-Biol. Chem. 5, 62–71.

Mummey, D.L., Smith, J.L., Bolton Jr., H., 1997. Small-scale spatial and temporal variability of N_2O flux from a shrub-steppe ecosystem. Soil Biol. Biochem. 29, 1699–1706.

Panek, J.A., Matson, P.A., Ortiz-Monasterio, I.P., Brooks, P., 2000. Distinguishing nitrification and denitrification sources of N_2O in a Mexican wheat system using ^{15}N. Ecol. Applications 10, 506–514.

Pulleman, M., Tietama, A., 1999. Microbial C and N transformations during drying and rewetting of coniferous forest floor material. Soil Biol. Biochem. 31, 275–285.

Robertson, G.P., Wedin, D., Groffman, P.M., Blair, J.M., Holland, E.A., Nadelhoffer, K.J., Harris, D., 1999. Soil carbon and nitrogen availability: nitrogen mineralization, nitrification, and soil respiration potentials. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), Standard Soil Methods for Long-Term Ecological Research. Oxford University Press, Inc., New York, pp. 264–265.

Rochette, P., Angers, D.A., Bélanger, G., Chantigny, M.H., Prévost, D., Lévesque, G., 2004. Emissions of N_2O from alfalfa and soybean crops in eastern Canada. Soil Sci. Soc. Am. J. 68, 493–506.

Schjønning, P., Thomsen, I.K., Moldrup, P., Christensen, B.T., 2003. Linking soil microbial activity to water- and air-phase contents and diffusivities. Soil Sci. Soc. Am. J. 67, 156–165.

Soon, Y.K., Haq, A., Arshad, M.A., 2007. Sensitivity of nitrogen mineralization indicators to crop and soil management. Comm. Soil Sci. Plant Anal. 38, 2029–2043.

Steenwerth, K.L., Belina, K.M. Cover crops enhance soil organic matter, carbon dynamics and microbiological function in a Mediterranean vineyard agroecosystem. Appl. Soil Ecol., in press.

Steenwerth, K.L., Jackson, L.E., Calderón, F.J., Scow, K.M., Rolston, D.E., 2005. Response of microbial community composition and activity in agricultural and grassland soils after a simulated rainfall. Soil Biol. Biochem. 37, 2249–2262.

Tiedje, J., 1994. Denitrifiers. In: Bigham, J.M., Mickelson, S.H. (Eds.), Methods of Soil Analysis. Part 2. Microbiological and Biochemical Properties. Soil Science Society of America, Madison, WI, USA.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass-C. Soil Biol. Biochem. 19, 703–707.

Venterea, R.T., Rolston, D.E., 2000. Mechanisms and kinetics of nitric and nitrous oxide production during nitrification in agricultural soil. Glob. Change Biol. 6, 303–316.

Waring, S.A., Bremner, J.M., 1964. Ammonium production in soil under waterlogged conditions as index of nitrogen availability. Nature 201 951-&.

Wyland, L.J., Jackson, L.E., Chaney, W.E., Klonsky, K., Koike, S.T., Kimple, B., 1996. Winter cover crops in a vegetable cropping system: impacts on nitrate leaching, soil water, crop yield, pests and management costs. Agric. Ecosyst. Environ. 59, 1–17.

Wu, J., Joergensen, R.G., Pommerening, B., Chaussod, R., Brookes, P.C., 1990. Measurement of soil microbial biomass C by fumigation extraction—an automated procedure. Soil Biol. Biochem. 22, 1167–1169.